

Cranial Shape in Fruit, Nectar, and Exudate Feeders: Implications for Interpreting the Fossil Record

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ABSTRACT At least 29 species of fossil primates have been referred to fruit, nectar, and/or exudate feeding dietary niches. Many studies have detailed the morphological correlates of fruit feeding in comparison to insectivory and folivory. In contrast, few studies have sought to differentiate the morphological correlates of fruit feeding from those of nectar and exudate feeding. This study investigates the differences between fruit, nectar, and exudate feeders using 22 cranial and dentary shape variables representing 28 species of living marsupials, bats, and primates. Discriminant function analysis is used to investigate the differences between these dietary categories using both the complete data set and a reduced data set composed of variables that might reasonably be available from fragmentary fossil material. The success rates of post-hoc classifications are 94 and 88%, respectively. These results demonstrate that it is possible to discriminate among fruit, nectar, and exudate feeders among fossil taxa with a reasonable degree of certainty using the data and techniques outlined here. Nectar feeders exhibit a unique combination of features that are associated with reduced masticatory strength and their role as pollination agents. Exudate feeder skulls and dentaries exhibit a combination of features that reflect the high stresses encountered by the anterior dentition through bark gouging behavior. Fruit feeders are morphologically diverse, exhibiting cranial and mandibular shape values that overlap with both nectar and exudate feeders. It is suggested that this diversity reflects the variety of physical properties represented among fruits, and the tendency for individual frugivore species to specialize on particular fruits. *Am J Phys Anthropol* 102:187-202, 1997 © 1997 Wiley-Liss, Inc.

Because broadly defined aspects of foraging ecology can be inferred from dietary habits (Janson and Boinski, 1992), reconstructing the dietary adaptations of fossil primates has long been a goal of primatological research. Such information has been fundamental in developing hypotheses of primate origins and diversification (e.g., Cartmill, 1972, 1974; Rasmussen, 1990; Beard, 1990, 1991; Sussman, 1991). Many aspects of mammalian dietary habits are reflected in the form of the skull, jaws, and teeth, and a multitude of analytic techniques have been used to investigate the dietary adaptations of primates, including

analyses of dental microwear (e.g., Teaford and Walker, 1984; Walker and Teaford, 1989; Ungar, 1990), tooth enamel morphology (e.g., Maas, 1993; Dumont, 1995; Teaford and Maas, 1995), tooth size and shape (e.g., Hylander, 1975; Kay, 1975; Strait, 1993a), and jaw architecture (e.g., Hylander, 1979; Ravosa, 1991; Anapol and Lee, 1994).

Primarily through the efforts of dental morphologists, techniques have been developed to infer dietary habits for animals that specialize on fruit, insects, and leaves. In-

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deed, several researchers are successfully developing methods of subdividing fruit and insect feeding based on the physical properties of food items (Freeman, 1979, 1981, 1988; Strait, 1993b; Anapol and Lee, 1994). In contrast to these relatively well-documented dietary categories, morphological correlates of nectivory and exudate feeding have received less attention, particularly with respect to the fossil record.

Morphological analyses of nectar and exudate feeding have been neglected primarily because there are relatively few easily recognizable morphological features separating them from fruit feeders. In addition, these strategies are relatively rare among living primates. Although exudate feeders are characterized by derived features of the anterior dentition (see review in Nash, 1986), they are not distinguishable from fruit feeders in details of molar morphology (Kay, 1984; Kay and Covert, 1984). Similarly, aside from the observation that nectar feeders have small teeth and relatively long dentaries (e.g., Freeman, 1988, 1995), no study has detailed the ways in which they differ from fruit or exudate feeders. Despite these difficulties in differentiating among fruit, nectar, and exudate feeders (especially without complete specimens), at least 29 species of fossil primates and plesiadapiforms have been referred to one or more of these dietary niches on the basis of dental and dentary morphology (Gingerich, 1976; Szalay and Delson, 1979; Covert, 1986; Kay, 1994; Williams and Covert, 1994; Beard, 1991).

In order to establish more firmly methods of identifying dietary adaptations among fossil species, this study seeks to develop a comparative database describing aspects of cranial and dentary shape that are specific to living fruit, nectar, and exudate feeding mammals. Two hypotheses are evaluated using this database. The first hypothesis is that skull and dentary shape variables can be used to discriminate between living fruit, nectar, and exudate feeding mammals. The second hypothesis is that a relatively small subset of these shape variables (such as might be available from fragmentary fossil material) can be used to assign fossil species to one of these dietary categories with a reasonable probability of success.

MATERIALS AND METHODS

Twenty-eight fruit, nectar, and exudate specialists were selected from the orders Marsupialia, Primates, and Chiroptera (Table 1). Where possible, phylogenetically diverse species were included in each dietary category to highlight anatomical features that are correlated with dietary habit and to minimize emphasis on features that characterize closely related species.

The category "nectar feeders" contains species that rely on nectar as a dietary staple throughout the year. Most species included in this category exhibit derived features of the tongue and/or gut that reflect their nectivorous habits (Arroyo-Cabrales et al., 1987; Howell and Hodgkin, 1976; Kingdon, 1974; McKean, 1983; Phillips, 1977; Richards, 1983; Turner, 1983). Most nectar feeders consume incidental insects, and some augment their diet (especially during the dry season) with smaller proportions of fruit and/or insects (see references in Table 1). For the present analysis, the category "exudate feeders" is limited to plant exudate specialists that engage in bark-gouging behavior in order to initiate sap flow. Opportunistic exudate feeders (e.g., *Saguinus* spp., *Perodicticus potto*) are not included in this category. As in other analyses (Freeman, 1988; Strait, 1993a), the category "fruit feeders" includes animals for whom fruit constitutes the largest proportion of the diet. Among the fruit feeders included in this study, nonfruit dietary supplements include insects, buds, nectar, pollen, leaves, and, occasionally, small vertebrates (see references in Table 1).

Twenty-two linear variables representing the skull and dentary were measured from 131 specimens housed at the Carnegie Museum of Natural History, the National Museum of Natural History (NMNH), and the British Museum of Natural History (Fig. 1). Measurements were made to the nearest 0.1 mm using digital calipers (Mitutoyo[®]). Each measurement was repeated and the original value accepted if the first and second values differed by no more than 3%. When more than 3% error was encountered, the measurement was repeated five times, the lowest and highest values were deleted, and the

TABLE 1. Species included in this study listed according to dietary category (i.e., fruit, nectar, and exudate feeders)¹

Taxon	N♀	N♂	Mass	Dietary references
Fruit feeders				
Order Chiroptera				
<i>Centurio senex</i>	1	3	41g ^{2,**}	Goodwin and Greenhall (1961)
<i>Platyrrhinus helleri</i>	3	1	13.43g [*]	Fleming et al. (1972)
<i>Pygoderma bilabiatum</i>	1	1	18.5g ^{2,**}	Myers (1981)
<i>Sturnira lilium</i>	5	5	25.85g ^{3,*}	Fleming et al. (1972); Heithaus et al. (1975)
<i>Artibeus jamaicensis</i>	5	6	49.8g ^{4,*}	Fleming et al. (1972); Heithaus et al. (1975)
<i>Carollia perspicillata</i>	5	5	17.6g ⁵	Fleming et al. (1972); Heithaus et al. (1975); Fleming (1988)
<i>Perodicticus potto</i>	1	3	1,150g ⁶	Charles-Dominique (1977); Oates (1984)
<i>Eidolon helvum</i>	4	2	200g ⁸	Funmilayo (1976)
<i>Epomophorus gambianus</i>	4	4	111.75g ^{8,**}	Thomas and Fenton (1978); Marshall and McWilliam (1982)
<i>Rousettus aegyptiacus</i>	3	5	117.4g ^a	Kingdon (1974); Thomas and Fenton (1978)
Order Marsupialia				
<i>Caluromys philander</i>	1	1	300g ⁷	Artamentowicz (1982); Charles-Dominique (1983)
Order Primates				
<i>Microcebus murinus</i>	1	1	70g ³	Hladik et al. (1980)
<i>Saguinus fuscicollis</i>	1	1	462g ^{3,*}	Crandemire-Sacco (1988); Garber (1988)
Nectar feeders				
Order Chiroptera				
<i>Anoura geoffroyi</i>	5	5	14g ^{3,*}	Howell and Burch (1974); Sazima (1976)
<i>Glossophaga soricina</i>	5	5	9.4g ³	Heithaus et al. (1975); Bonaccorso (1979)
<i>Choeronycteris mexicana</i>	1	1	15g ^{12,**}	Howell and Burch (1974)
<i>Erophylla sezekorni</i>	1	1	19.2g ^{****}	Silva-Taboada and Pine (1969)
<i>Leptonycteris nivalis</i>	2	2	24g ¹³	Dahlquest (1953); Schmidley (1991)
<i>Macroglossus minimus</i>	1	1	14g ¹⁴	McKean (1983); Mickleburgh et al. (1992)
<i>Megaglossus woermanni</i>	1	1	16g ¹⁵	Kingdon (1974); Mickleburgh et al. (1992)
<i>Syconycteris australis</i>	1	1	15g ¹⁶	Richards (1983)
<i>Micropterus pusillus</i>	5	5	30g ¹⁵	Marshall and McWilliam (1982)
Order Marsupialia				
<i>Cercartetus nanus</i>	1	1	24g ¹⁰	Turner (1983, 1984a)
<i>Acrobates pygmaeus</i>	—	1	12g ^{11,**}	Russell (1983); Turner (1984b)
Exudate feeders				
Order Marsupialia				
<i>Petaurus breviceps</i>	1	1	127.5g ^{17,*}	Smith (1982); Howard (1989)
Order Primates				
<i>Euoticus elegantulus</i>	2	2	274g ^{6,*}	Charles-Dominique (1977)
<i>Callithrix jacchus</i>	2	1	310g ^{6,*}	Rylands and de Faria (1993)
<i>Cebuella pygmaea</i>	1	1	135g ^{6,*}	Rylands and de Faria (1993)

¹ N♂, number of males; N♀, number of females; Mass, body mass estimates.

² Emmons, 1990; ³ Eisenberg, 1989; ⁴ Handley et al., 1991; ⁵ Eisenberg, 1981; ⁶ Fleagle, 1988; ⁷ Charles-Dominique, 1983; ⁸ Boulay and Robbins, 1989; ⁹ Coe, 1975; ¹⁰ Turner, 1983; ¹¹ Russell, 1983; ¹² Arroyo-Cabrales et al., 1987; ¹³ Pirimner-Hensley and Wilkins, 1988; ¹⁴ McKean, 1983; ¹⁵ Kingdon, 1974; ¹⁶ Richards, 1983; ¹⁷ Suckling, 1983.

* Combined male and female mean values.

** Midpoint of reported range(s).

*** Midpoint of seasonal means.

**** Mean values from NMNH specimen tags (N♀ = 3; N♂ = 3).

mean of the remaining three values was used to represent that specimen.

The data collected for this study are characterized by unequal sample sizes both among species and between sexes within species. To eliminate the potential impact of unequal sample size while maintaining some representation of variance within species, most species were represented by male and female mean values. Three species were represented by only one set of values. Female specimens of *Acrobates pygmaeus* were not available for study. Single values were missing from either male or female data sets

for samples of *Microcebus murinus* and *Saguinus fuscicollis*. Rather than delete these specimens from the analysis, data collected from males and females were combined in single sets of values to represent each species. After these adjustments for unequal sample size and missing data, the resulting data matrix contained values representing 51 samples (representatives of males and females for most species) and 22 linear skull and dentary variables.

Because this analysis includes species that range in body size from 9 to 1,150 g (Table 1), data contained within the sample by vari-

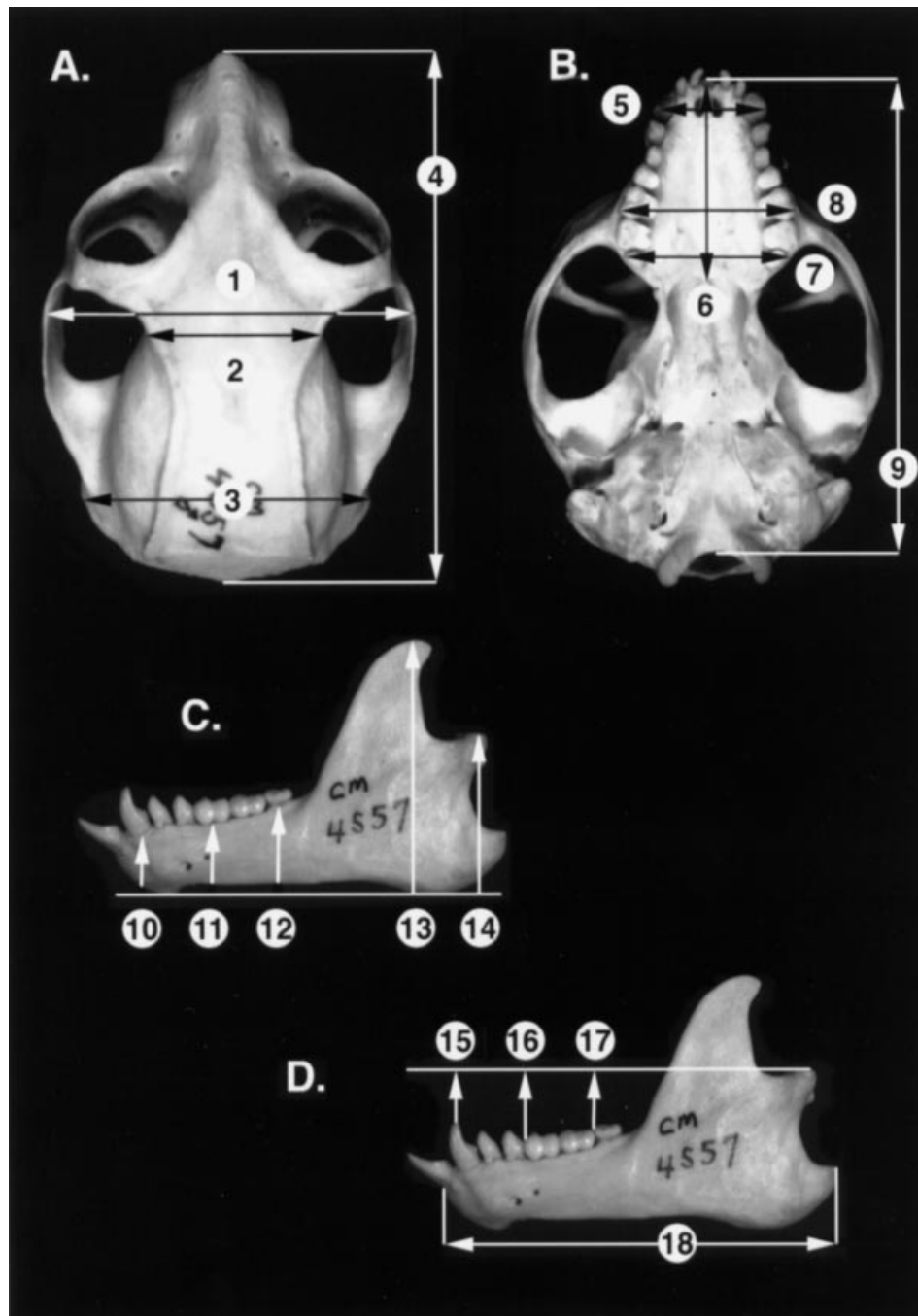


Fig. 1. Skull and dentary variables used in this study. All variables were included in the complete data set. Variables listed in bold were included in the fossil data set. **A:** Dorsal view of a *Perodicticus potto* cranium illustrating: (1) maximum zygomatic breadth (MZB), (2) minimum skull width at temporal fossae (MSW), (3) maximum posterior skull width (PSW), and (4) total skull length (TSL). **B:** Ventral view of a *Perodicticus potto* cranium illustrating: (5) **palate width at canines (APW)**, (6) **total palate length (TPL)**, (7) **palate width at M3 (PPW)**, (8) **palate width at M1 (MPW)**, and (9) anterior skull length (ASL). **C:** Lateral view of *Perodicticus potto* dentary illustrating: (10)

dentary depth at canine (CDD), (11) **dentary depth at m1 (MDD)**, (12) **dentary depth at m3 (PDD)**, (13) **coronoid process height (CPH)**, and (14) **condyle height (CH)**. **D:** Lateral view of dentary of a *Perodicticus potto* dentary illustrating: (15) condylocanine length (CC), (16) **condyle to m1 length (CM1)**, (17) **condyle to m3 length (CM3)**, and (18) total dentary length (TDL). Measurements included in this study but not pictured here are skull height (SH), **maximum condyle length (CL)**, **maximum condyle width (CW)**, and **m2 area (AREA)** (maximum length \times width).

able matrix were transformed to shape data using the geometric mean technique developed by Darroch and Mosiman (1985) and employed by Falsetti et al. (1993) and Anapol and Lee (1994). This technique adjusts for size on a sample-by-sample basis to provide self-adjusted estimates of shape (in contrast to the sample-adjusted estimates provided by regression residuals). For each sample, the transformation is accomplished by calculating the geometric mean of all variables and then dividing each variable by that geometric mean. The natural logs of the shape-transformed variables were used in subsequent analyses.

To address the hypothesis that living fruit, nectar, and exudate feeders can be differentiated on the basis of cranial shape, the complete data set containing 22 skull and dentary variables was analyzed. Stepwise discriminant function analysis was used to identify variables that are significant in distinguishing between the three dietary categories. In this analysis, a significance level to enter/remove of 0.05 (based on an F-test from an analysis of covariance) was used to sequentially enter and delete variables in the analysis (SAS® User's Guide, 1985; Tabachnick and Fidell, 1989). Canonical discriminant function was employed to summarize the distribution of species based on these variables. Finally, variables with significant discriminating power were entered into a direct discriminant function analysis to evaluate the post hoc ability of the discriminant function derived from them to correctly classify species with respect to dietary category. In conjunction with inspection of group means, a posteriori multiple comparisons tests were used to investigate the pattern of differences between the three dietary categories (Tabachnick and Fidell, 1989).

To assess the hypothesis that a limited data set can reliably distinguish among fruit, nectar, and exudate feeders, the identical sequence of analyses was repeated using a reduced data set containing 14 measurements that might reasonably be available from well-represented, though fragmentary, fossil material (Fig. 1). Variables included in this simulated fossil data set reflect the shape of the palate and the posterior portion

of the dentary; more encompassing skull measurements were excluded because complete and undistorted fossil crania are rare. Size adjustments were recalculated using only the variables in this reduced data set.

RESULTS

The stepwise discriminant function analysis of all cranial and dentary measurements identified eight variables that, in the presence of one another, contribute significantly to differentiating fruit, nectar, and exudate feeders ($P < 0.05$, analysis of covariance F-test). In order of their entry into the analysis these are: total skull length, condylo-canine length, total dentary length, middle skull width, dentary depth at the canine, coronoid process height, posterior skull width, and tooth area. Canonical discriminant function analysis of these eight variables yielded two functions that accounted for 87 and 13%, respectively, of the between-group variability of the three categories ($P < 0.001$, Pillai's criterion). Figure 2 demonstrates that the first discriminant function separates fruit feeders from nectar and exudate feeders. The second discriminant function separates nectar and exudate feeders, while fruit feeders are distributed across both of these groups.

The correlations between each variable and the two discriminant functions are presented in Table 2. Based on these values, tooth area is important in separating fruit feeders from nectar and exudate feeders on the first discriminant function. Fruit feeders have relatively larger teeth than nectar and exudate feeders (group means for all variables are presented in Table 3). Both total skull length and coronoid process height are correlated with the first discriminant function with reasonably high values (.56 and $-.32$, respectively). While these results demonstrate that fruit feeders have relatively short skulls and tall coronoid processes in comparison to exudate and nectar feeders combined, both skull length and coronoid process height exhibit higher correlation with the second discriminant function. Variables important in discriminating between nectar and exudate feeders (function 2) are total skull length, posterior skull width, middle skull width, coronoid process height,

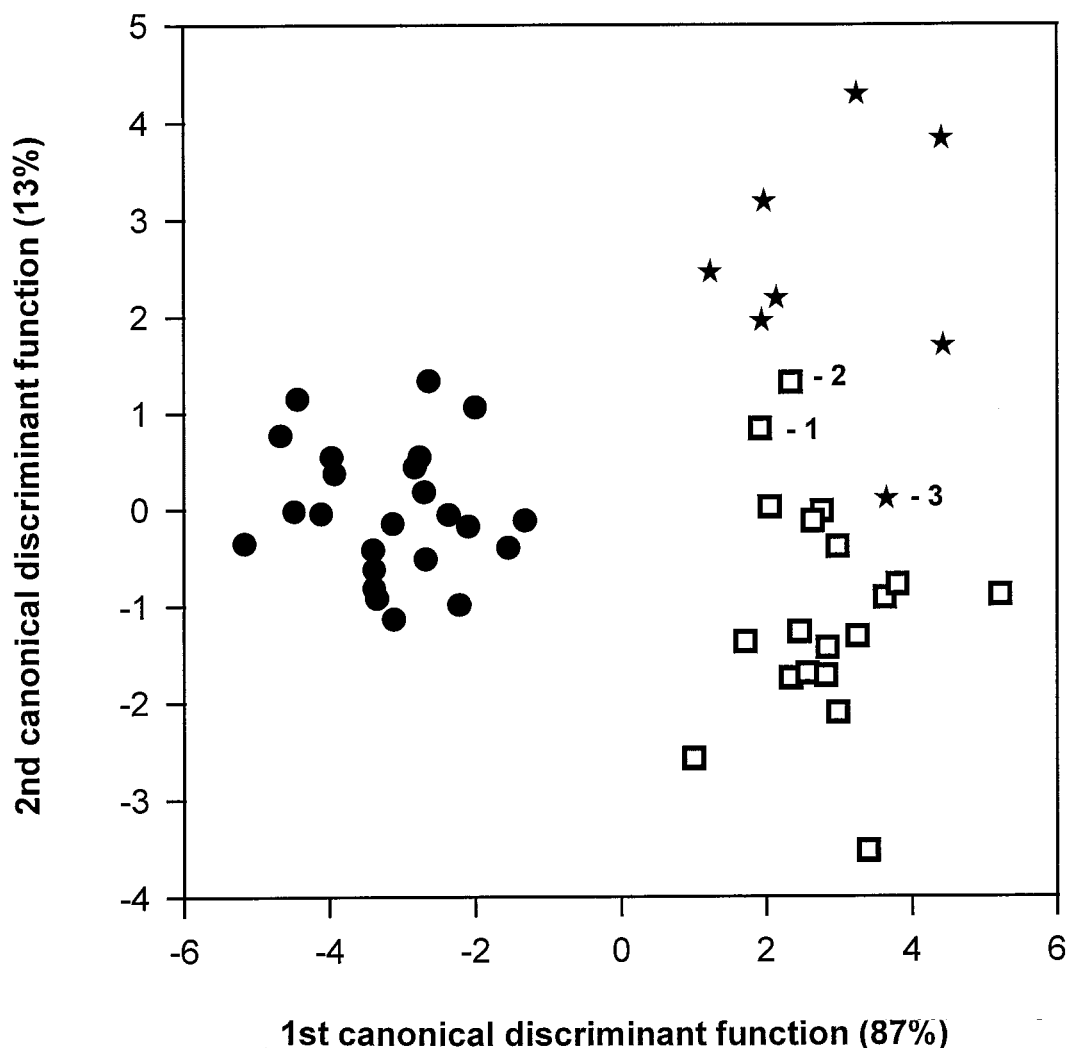


Fig. 2. Discrimination of fruit (●), nectar (□), and exudate feeders (★) based on canonical discriminant analysis of eight cranial and mandibular shape variables from the complete data set. The percent of variance explained by each axis is given in parentheses.

Post-hoc classification using direct discriminant function analysis resulted in the misclassification of male and female *Cercartetus nanus* (1 and 2) as exudate feeders, and of male *Petaurus breviceps* (3) as nectar feeders.

condyle-canine length, and total dentary length. Nectar feeders have relatively long skulls and dentaries, while exudate feeders have relatively wide skulls and high coronoid processes. Correlations smaller than 0.30 are not interpreted (Tabachnick and Fidell, 1989).

The results of all pairwise a posteriori multiple comparisons tests (GT2) between the dietary categories are presented in Table 3 (Sokal and Rohlf, 1981). Nectar feeders

exhibit significantly longer skulls and dentaries and relatively lower coronoid processes than fruit and exudate feeders. Each dietary category differs significantly from the others in condylocanine length; exudate feeders have the shortest dentaries and nectar feeders the longest. Exudate feeders exhibit significantly greater middle skull width than both fruit and nectar feeders. Posterior skull width is also significantly greater in exudate feeders than in fruit

TABLE 2. Results of canonical discriminant function analysis of variables selected from the complete data set by stepwise discriminant procedures

Predictor variable ¹	Correlations with discriminant functions		Univariate F [F(2,48)]	Pooled within-group correlations among variables						
	1	2		PSW	MSW	CDD	CPH	CC	TDL	AREA
TSL	.56	-.68	29.53***	-.32*	-.24	-.12	-.19	.88***	.85***	-.06
PSW	.24	.40	4.08*		.46***	.39**	-.53***	-.62***	-.69***	.53***
MSW	.19	.55	6.39**			.40**	-.39*	-.24	-.32*	-.03
CDD	-.26	-.05	1.56				-.11	-.36**	-.37**	.09
CPH	-.32	.44	6.46*					-.06	-.04	-.62***
CC	.17	-.74	12.69***						.98***	-.22
TDL	.28	-.71	14.37***							-.29*
AREA	-.46	-.08	5.95**							
Canonical R	.95	.77								
Eigenvalue (R ²)	.90	.59								
R ² /(1-R ²)	9.38	1.43								

¹ TSL = total skull length, PSW = maximum posterior skull width, MSW = minimum skull width at temporal fossae, CDD = dentary depth at canine, CPH = coronoid process height, CC = condylocanine length, TDL = total dentary length, AREA = m2 area.

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.00$.

TABLE 3. Means and standard errors of raw cranial and dentary shape variables that contribute significantly to discriminating among fruit, nectar, and exudate feeders¹

Shape variable	Nectar feeders (N = 19)	Fruit feeders (N = 24)	Exudate feeders (N = 8)
Complete data set			
CC	[2.99 ± 0.505]	[2.56 ± 0.399]	[2.15 ± 0.127]
TSL	[4.59 ± 0.487]	[3.83 ± 0.257]	[3.79 ± 0.178]
CPH	[0.97 ± 0.184]	[1.16 ± 0.226]	[1.17 ± 0.132]
TDL	[3.17 ± 0.476]	[2.65 ± 0.411]	[2.35 ± 0.049]
MSW	[0.99 ± 0.198]	[.01 ± 0.289]	[1.48 ± 0.466]
PSW	[1.89 ± 0.214]	[1.85 ± 0.315]	[2.15 ± 0.141]
AREA	[0.17 ± 0.029]	[0.21 ± 0.047]	[0.18 ± 0.013]
CDD	[0.30 ± 0.043]	[0.54 ± 0.754]	[0.28 ± 0.060]
Fossil data set			
TPL	[4.03 ± 0.827]	[2.40 ± 0.405]	[2.75 ± 0.779]
CL	[0.49 ± 0.09]	[0.43 ± 0.054]	[0.56 ± 0.079]
CH	[1.09 ± 0.196]	[1.38 ± 0.282]	[1.07 ± 0.253]
AREA	[0.29 ± 0.046]	[0.29 ± 0.030]	[0.33 ± 0.074]
CPH	[1.58 ± 0.249]	[1.87 ± 0.175]	[1.81 ± 0.334]

¹ For each variable, values within brackets are statistically distinct from other (sets of) values (based on GT2 tests of size-adjusted, logged variables). For example, within the complete data set tooth area differs significantly between nectar feeders and fruit feeders, while exudate tooth area values do not differ significantly from those of the other dietary categories. CC = condylocanine length, TSL = total skull length, CPH = coronoid process height, TDL = total dentary length, PSW = maximum posterior skull width, AREA = m2 area, CDD = dentary depth at canine, TPL = total palate length, CL = maximum condyle length, CH = condyle height.

feeders; nectar feeders' skulls are most similar to fruit feeders in this dimension. Fruit feeders have significantly larger teeth than nectar feeders, while exudate feeders exhibit intermediate relative tooth size values.

Dentary depth at the canine does not differ significantly among the three dietary categories in the absence of covariance with other variables (although fruit feeder mean values are largest and those of nectar and exudate feeders are very similar to one another).

Inspection of the pooled within-group correlations among the variables (Table 2) illustrates that species with relatively wide skulls have relatively low coronoid processes, short dentaries, and deep mandibles. Relatively short dentaries tend to be deep. While tooth area increases significantly with posterior skull width, it decreases with coronoid process height and total dentary length. Not unexpectedly, most measurements that reflect overall skull length and width are significantly correlated.

The direct discriminant function derived from these eight variables correctly classified species into the appropriate dietary category in 94% (48 of 51) of cases. Males and females of the nectar feeding species *Cercartetus nanus* were classified as exudate feeders, and one exudate feeder (male *Petaurus breviceps*) was classified as a nectar feeder (Fig. 2).

Of the 14 variables included in the fossil data set, stepwise discriminant function analysis identified five that contribute significantly to segregating fruit, nectar, and exudate feeders ($P < 0.05$, analysis of covariance F-test). These variables are: total palate length, condyle height, coronoid process

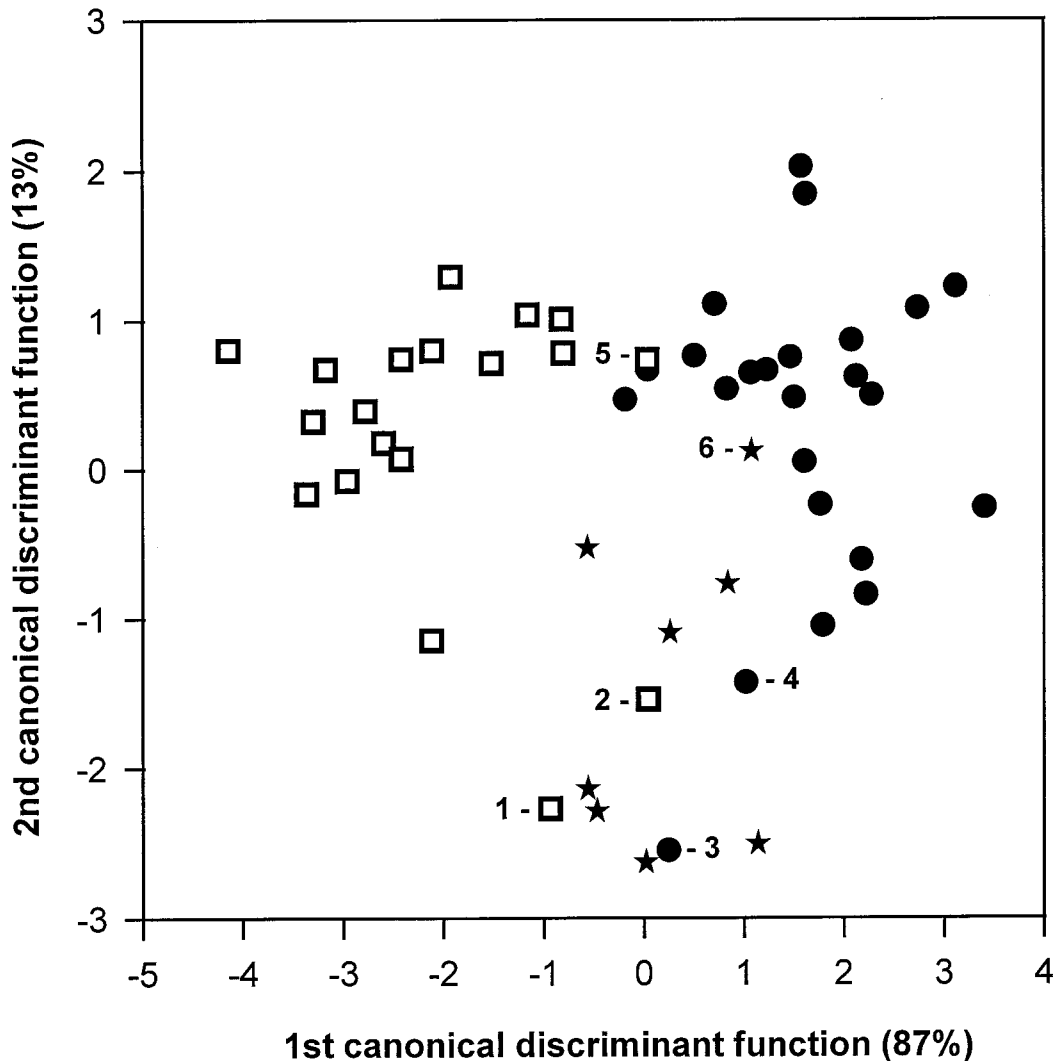


Fig. 3. Discrimination of fruit (●), nectar (□), and exudate (★) feeders based on canonical discriminant analysis of five palate and mandibular shape variables from the fossil data set. The percent of variance explained by each axis is given in parentheses. Post-hoc classification using direct discriminant function analysis

resulted in the misclassification of male and female *Cercartetus nanus* (1 and 2), *Microcebus murinus* (3), and *Saguinus fuscicollis* (4) as exudate feeders, and of male *Syconycteris australis* (5) and male *Petaurus breviceps* as fruit feeders (6).

height, condyle length, and tooth area. Canonical discriminant function analysis of these five variables yielded two functions that explain 87 and 13%, respectively, of the between-group variation among the samples ($P < .0001$, Pillai's criterion). Figure 3 illustrates that the first function separates nectar feeders from exudate and fruit feeders, while the second function discriminates be-

tween exudate feeders and most fruit and nectar feeders.

Correlations between each variable and the two discriminant functions are presented in Table 4. On the first axis, the variables total palate length, tooth area, and coronoid process height are important in separating nectar feeders from the other two groups. In contrast to fruit and exudate

TABLE 4. Results of canonical discriminant function analysis of variables selected from the fossil data set by stepwise discriminant procedures¹

Predictor variable	Correlations with discriminant functions		Univariate F [F(2,48)]	Pooled within-group correlations among variables			
	1	2		CH	CPH	CL	AREA
TPL	-.69	.52	18.00***	.02	.21	.21	-.19
CH	-.05	-.75	4.96**		.70***	-.29*	-.46***
CPH	.40	-.36	4.52*			-.32*	-.74***
CL	.34	.70	7.49**				.17
AREA	.37	.23	3.16*				
Canonical R	.86	.55					
Eigenvalue (R ²)	.74	.30					
R ² /(1-R ²)	2.82	.43					

¹ TPL = total palate length, CH = condyle height, CPH = coronoid process height, CL = maximum condyle length, AREA = m2 area.

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.00$.

feeders, nectivores have relatively longer palates, smaller teeth, and lower coronoid processes. The variables condyle height, condyle length, total palate length, and, to a lesser extent, coronoid process height are correlated with the second discriminant function. On this dimension, exudate feeders differ from fruit and nectar feeders in having relatively short palates and condylar articular surfaces in combination with relatively high condyles and coronoid processes.

The pooled within-group correlation coefficients presented in Table 4 reveal that relatively long mandibular condyles are significantly associated with relatively low condyles and coronoid processes. Similarly, as tooth area increases, condyle and especially coronoid process height decrease. Condyle height and coronoid process height exhibit strong positive correlation.

Results of a posteriori multiple comparisons tests of significantly discriminating variables ($P < 0.05$, GT2 test) are presented in Table 3. Two of the variables included in this fossil data set were also part of the larger complete data set. Within each of these data sets, tooth area and coronoid process height illustrate the same patterns of difference between the dietary categories despite the fact that they were transformed using different size estimates (i.e., geometric means based on different sets of variables). In each data set, nectar feeders exhibit the relatively smallest teeth and lowest coronoid processes. Fruit feeders have the largest teeth, and exudate feeders display the tallest coronoid processes. The similarity in

the pattern of differences in these values provides confirmation that shape variables contained within each data set are comparable.

Among the variables unique to the fossil data set, nectar feeders are distinctive in having significantly longer palates than fruit and exudate feeders. Exudate feeders have relatively tall mandibular condyles in comparison to the other groups, and fruit feeders exhibit significantly longer condyles than either exudate or nectar feeders.

The function derived from direct discriminant analysis of the fossil data set was able to correctly classify 88% (48 of 51) of cases. Figure 3 illustrates that males and females of the nectivorous *Cercartetus nanus* were misclassified as exudate feeders, while male *Syconycteris australis* were misclassified as fruit feeders. The fruit feeding primates *Microcebus murinus* and *Saguinus fuscicollis* were misclassified as exudate feeders. Finally, males of the exudate feeding marsupial *Petaurus breviceps* were misclassified as fruit feeders. Table 5 presents the discriminant function coefficients and constants used to perform this classification.

DISCUSSION

This analysis supports the hypothesis that cranial and dentary shape values can be used to discriminate effectively among living fruit, nectar, and exudate feeding mammals. A discriminant function derived from eight of the original 22 variables was used to successfully classify 94% of the sample. Within this sample, fruit feeders are well

TABLE 5. Discriminant function coefficients and constants for variables in the fossil data set¹

Variables	Discriminant function coefficients		
	Fruit feeders	Nectar feeders	Exudate feeders
TPL	14.89	24.99	15.51
CH	-16.06	-6.15	-6.18
CPH	-10.96	-45.96	-27.46
CL	-24.87	-36.06	-33.44
AREA	-39.91	-56.82	-47.27
CONSTANT	-33.66	-55.78	-40.99

¹ These data can be used to predict group membership of new cases (see Appendix). TPL = total palate length, CH = condyle height, CPH = coronoid process height, CL = maximum condyle length, AREA = m2 area.

separated from the other groups and misclassification occurs among a small number of nectar and exudate feeding marsupials (Fig. 2). This appears to represent a real overlap in the morphology of exudate and nectar feeders, as the dietary habits and feeding behavior of both *Cercartetus nanus* and *Petaurus breviceps* are well documented (e.g., Henry and Suckling, 1984; Smith, 1982; Turner, 1984a). Other marsupials in the sample are embedded well within their proper dietary category.

The post hoc classification of the limited fossil data set was less successful (88% classified correctly). Nevertheless, the hypothesis that data summarizing palate and mandibular shape can effectively discriminate between fruit, nectar, and exudate feeders can be accepted. In contrast to the previous analysis, nectar feeders are more tightly clustered than are fruit or exudate feeders (Fig. 3). Misidentifying nectar and fruit feeders as exudate feeders (i.e., *Cercartetus nanus*, *Microcebus murinus*, *Saguinus fuscicollis*) is the most frequent form of misclassification. Other misclassifications include identifying a single nectar feeder (male *Synonycteris australis*) and a single exudate feeder (male *Petaurus breviceps*) as a fruit feeder.

Analyses of each of the data sets demonstrate that fruit feeders are less specialized and exhibit greater morphological diversity than either nectar or exudate feeders. Variables included in the analysis of the complete data set reflect large-scale measurements of skull and dentary length, depth, and width. Along the first axis, which segre-

gates fruit feeders from nectar and exudate feeders, only tooth area exhibits significant loadings that are larger than loadings on the second axis. While the second axis provides good separation between nectar and exudate feeders on the basis of six variables, fruit feeders overlap with both dietary categories. Within the fossil data set, fruit feeders exhibit even broader overlap with nectar and exudate feeders. Increased condyle length is the only feature that distinguishes fruit feeders from the other two groups.

Although the shape variables that emerged as significant in this analysis are not pure functional approximations of cranial and dentary mechanical efficiency, a variety of functional correlates can be suggested to account for the shape differences encountered between the three groups. A consideration of these differences (summarized in Table 3) may also shed light on the patterns of misclassification and morphological diversity among frugivores encountered in both of the data sets.

The nectar feeders in this sample are characterized by relatively long skulls, dentaries, and palates. These features are often associated with carnivory (and in some cases insectivory), where they are part of a suite of features associated with prey grasping and killing (Freeman, 1979; Radinsky, 1981a,b). In contrast to carnivores, nectar feeders generally lack extensive muscle insertions, shearing teeth, and re-enforced temporomandibular joints (Rosenberg and Richardson, 1995; Storch, 1969). For example, within this study nectar feeders exhibit significantly shorter (in fact, poorly developed) coronoid processes than either fruit or exudate feeders, indicating the minor role of the masticatory muscles that attach to it in nectar feeding. In the context of nectar feeding, the long condyle to canine distances appear to be indicative of relatively inefficient transfer of force to the anterior dentition. The relatively small molar teeth of the nectar feeders again support the common conclusion that nectar feeders have a reduced masticatory apparatus in response to a primarily liquid diet (e.g., Freeman, 1988, 1995; Hill and Smith, 1984; Rosenberg and Richardson, 1995). Rather than being dedicated to masticatory strength, the skulls

and dentaries of nectar feeders appear to reflect the role of these animals as pollination agents (e.g., Heithaus et al., 1975; Janzon et al., 1981; Wooller et al., 1984).

Many of the unique features of exudate feeder skulls and dentaries appear to reflect the increased stress placed on the anterior dentition through bark gouging. Exudate feeder skulls are significantly wider in the region of the temporal fossa than the skulls of either fruit or nectar feeders. Cartmill (1977) reported that a strengthened connection between the skull and facial skeleton via klinorhynch (an increased angle between the basicranium and palate) is characteristic of primates and marsupials that use the anterior dentition in bark gouging. The relatively wide skull at the junction between the braincase and face of exudate feeders may represent either a correlate of klinorhynch or serve a similar buttressing function. Exudate feeder skulls are also relatively wide posteriorly in the region of the attachment of nuchal musculature. As yet, no study has investigated whether these muscles function to stabilize the skull during bark preparation.

With respect to the exudate feeder dentary, the relatively short distances between the mandibular condyle and canine/incisor serve to move these bite points closer to the temporomandibular joint, increasing the efficiency of muscle forces transferred to the anterior dentition. Exudate feeder dentaries also exhibit an elevated mandibular condyle. Biomechanical analyses have demonstrated that elevated mandibular condyles (with respect to the occlusal plane) facilitate simultaneous occlusion of the cheek teeth and thereby evenly distribute masticatory forces across them (De Wolff-Exalto, 1951; Greaves, 1974). Some insights into the function of elevated condyles in exudate feeders might be gained from a consideration of dentary shape in bats.

Freeman (1979) demonstrated that elevated mandibular condyles (and concomitant increases in masseter size) are characteristic of bats that specialize in eating beetles, which are relatively hard and presumably require relatively high bite forces to fracture. Although exudate feeders are not known to be hard insect specialists,

similar demands for strong jaw adduction may be imposed by bark gouging. Both primate and marsupial exudate feeders prepare bark by placing the upper incisors against the substrate and scraping upwards with the lower incisors (Rylands, 1984; R. Goldingay, personal communication). Clearly this behavior requires strength in jaw adduction. Alternatively, using a broad taxonomic sample, Freeman (1984) illustrated that condyle height is negatively correlated with the degree of klinorhynch. While klinorhynch in bats is associated with the mode of sound emission (Pedersen, 1993), its relationship to the mechanical demands of food processing has not received detailed attention. Whether the relatively high condyles of exudate feeders are closely associated with relatively strengthened jaw adductors or are more strongly influenced by klinorhynch awaits a more specific analyses of the form and function of exudate feeder skeletal and muscular anatomy.

Of the three dietary categories, fruit feeders are the least morphologically distinct. In most measurements of skull shape, fruit feeders are indistinguishable from either nectar or exudate feeders (Table 3). They do, however, exhibit some interesting extremes in several aspects of dentary shape. Although fruit feeders typically possess smaller teeth than insectivores (Strait, 1993a), their teeth are relatively larger than those of either nectar or exudate feeders. Not unexpectedly, the trend in increasing tooth size from nectar feeders, through exudate feeders to fruit feeders, is correlated with an increase in food item resistance. While fruits can be quite hard and/or tough (Lucas and Corlett, 1991; Ungar, 1995), exudates are reported to be relatively soft (Nash, 1986) and nectar (and incidental insects) requires minimal comminution.

Within this sample, fruit feeders possess the lowest condyle height values. Among mammals, relatively low mandibular condyles are associated with both scissor-like occlusion (De Wolff-Exalto, 1951; Greaves, 1974) and increased gape (Herring and Herring, 1974; Wall and Krause, 1992). Each of these effects plays a role in frugivore food processing. Many studies have demonstrated that incisal preparation is a common compo-

nent of fruit feeding and the scissor-like occlusion may provide either more control over incision or permit larger forces to be exerted on the incisor teeth. Wide gape may permit fruit feeders to process relatively large fruits.

A relatively long mandibular condyle is the only unique feature of the frugivores in this sample. Comparative studies of primate mandibles demonstrate that frugivores have longer condyle articular surfaces than folivores and suggest that it is associated with emphasis on anterior tooth use (Bouvier, 1986; Smith et al., 1983). Within the present study, it is not apparent whether longer condyles reflect relatively larger condylar area (and relatively high joint reaction forces) or greater anteroposterior mobility of the temporomandibular joint (perhaps related to incisal preparation). The functional interpretation of increased condyle length in fruit feeders considered here awaits documentation of dentary corpus dimensions and the morphology of the glenoid cavity.

Clearly fruit, nectar, and exudate feeders differ in many aspects of cranial morphology that can be interpreted in light of known ecological roles and/or ingestive behaviors. However, this analysis also demonstrates that overlap exists between these categories. This is especially true of estimates of group membership derived from the fossil data set. While fruit and exudate feeders are never misclassified as nectar feeders (although nectar feeders are occasionally misclassified), exudate and fruit feeders are frequently mistaken for one another (Fig. 2). An explanation for this may reside in the proposition that some fruit feeders face mechanical demands that are similar to those encountered by exudate feeders. All exudate feeders routinely emphasize powerful dentary adduction, but the same may be true of fruit feeders that consume relatively large, hard, or tough fruits. In addition, some fruit and exudate feeders may include similar proportions of insects in their diets.

Frugivores as a group have diverse dietary preferences, but individual frugivorous species often exhibit specific fruit preferences (see, for example, Bonaccorso and Gush, 1987; Estrada et al., 1984; Fleming, 1986; Gauthier-Hion et al., 1985). It seems

likely that the wide range of masticatory morphology seen among frugivores is correlated with the range of physical properties seen in fruits as well as the proportion of insects that are consumed. Certainly, assessments of the physical properties of food items (i.e., size, hardness, toughness) could offer tremendous insights into the range of variation in cranial and mandibular morphology among frugivores.

The present study demonstrates that differentiable suites of cranial features characterize living fruit, nectar, and exudate feeding mammals. This result offers the opportunity to analyze fossil mammals in a similar manner. Indeed, analyses of the fossil data set presented here suggest that it would be possible to identify these cranial specializations among many early tertiary primates and plesiadapiforms. Although the cranial morphology of early primates and, especially, plesiadapiforms probably differs in detail from the taxa surveyed here, the purpose of this study is to interpret underlying similarities in the basic design of the masticatory apparatus, which is far more conserved (Smith, 1993). The combination of primates, bats, and marsupials is designed to highlight structural similarities regardless of higher-level group membership and provides a reasonable basis for interpreting the feeding adaptations of extinct mammals from many different mammalian orders.

The ability to generate dietary inferences for fossil specimens is one of the most intriguing applications of the data described in this study. Appendix 1 provides the information required to make such a prediction. However, in interpreting group membership for new material, it is essential to keep in mind that the post-hoc classification success rate using these data is only 88%, so that under the best of circumstances misclassification will occur in one of five cases. More specifically, while fruit and exudate feeders are never misidentified as nectar feeders, the identification of exudate and fruit feeders is more difficult. Thus, even with relatively complete material, dietary assignments for fossil taxa should be approached cautiously.

Finally, recent studies by Sussman (1991) and Beard (1990, 1991) propose that the emergence of Primates is associated with

adaptations to an expanding array of flowering plants during the Early Tertiary. Analyses such as this one may offer new insights into whether early members of the primate lineage were specialized plant feeders (Beard, 1990, 1991) or exhibited more omnivorous habits (Sussman, 1991). Data is currently being assembled to address this question and to offer a new and perhaps more detailed perspective on the ecological and adaptive context of primate origins.

CONCLUSIONS

Discriminant function analysis of 22 cranial and dentary shape variables demonstrates that a relatively small subset of variables can be used to reliably distinguish between living fruit, nectar, and exudate feeding mammals. These variables primarily reflect skull and dentary length, although tooth size and dentary height are also important discriminators. Results from an analysis of a more limited set of variables suggest that the variables and techniques outlined here will be useful interpreting dietary habits of fossil primates that have been classified as fruit, nectar, and/or exudate feeders. Within the fossil data set, palate length, condyle height and length, coronoid process height, and tooth area contribute significantly to distinguishing among fruit, nectar, and exudate feeders. Nevertheless, this study demonstrates that assigning a fragmentary fossil to one of these dietary categories remains a difficult endeavor.

An inspection of values that contribute to significant discrimination among the three dietary categories reveals patterns of differences between the groups for which functional correlates can be suggested. Overall, nectar and exudate feeders exhibit more specific cranial and mandibular morphologies than do fruit feeders.

Nectar feeders have relatively long skulls and dentaries, small teeth, and weakly defined coronoid processes. The delicate masticatory apparatus reflects a diet of liquid, pollen grains, and incidental insects. In addition, many studies have demonstrated that nectar feeders are vital pollination agents and it is likely that cranial morphology in these species is closely associated with flower morphology. Exudate feeders exhibit mor-

phological specializations that reflect the strength required to scrape bark and access saps. It is important to note that these specializations reflect bark gouging and not exudate feeding per se. The data presented here are not designed to differentiate between a bark gouging insectivore and a bark gouging exudate feeder. In contrast to nectar and exudate feeders, fruit feeders exhibit diversity in cranial and mandibular morphology (especially based on the fossil data set) that may reflect the variety of physical properties represented among fruits and the tendency for individual frugivore species to specialize on particular fruit species.

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APPENDIX

Within the context of the present study, to decide whether a new case should be classified as a fruit, nectar, or exudate feeder, measurements should be collected for the

following variables: TPL = total palate length, CH = condyle height, CPH = coronoid process height, CL = condyle length, and AREA = m² area (see Figure 1). Next, divide each measurement using the geometric mean of all of the variables for that specimen (Darroch and Mosiman, 1985), and then take the natural log of each size-adjusted measurement. These measurements are referred to as lnTPL, lnCH, etc. Next compute a classification function score for each of the categories; fruit feeder (F), nectar feeder (N) and exudate feeder (E) according to the following polynomials:

$$F = (14.89 \times \ln \text{TPL}) + (-16.06 \times \ln \text{CH}) \\ + (-10.96 \times \ln \text{CPH}) + (-28.87 \times \ln \text{CL}) \\ + (-39.91 \times \ln \text{AREA}) + (-33.66)$$

$$N = (24.99 \times \ln \text{TPL}) + (-6.15 \times \ln \text{CH}) \\ + (-45.96 \times \ln \text{CPH}) + (-36.06 \times \ln \text{CL}) \\ + (-56.82 \times \ln \text{AREA}) + (-55.78)$$

$$E = (15.51 \times \ln \text{TPL}) + (-6.18 \times \ln \text{CH}) \\ + (-27.46 \times \ln \text{CPH}) + (-33.44 \times \ln \text{CL}) \\ + (-47.27 \times \ln \text{AREA}) + (-40.99)$$

The group that results in the highest classification score is the most likely group to which the new case belongs. Note the warnings in the body of the paper regarding over-interpretation of this result.